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The remarkable Australian rove beetle genus *Myotyphlus*: its cryptic diversity and significance for exploring mutualism among insects and mammals (Coleoptera: Staphylinidae)

Running title: *Myotyphlus* and mutualism with mammals in rove beetles

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The remarkable Australian rove beetle genus *Myotyphlus*: its cryptic diversity and significance for exploring mutualism among insects and mammals (Coleoptera: Staphylinidae)

‘C'est un des types les plus curieux de l'immense famille des Staphylinides.’ [it is one of the most curious types of the vast family of rove beetles]. (Fauvel 1883)

‘*Myotyphlus* remains the most enigmatic genus.’ (Ashe & Timm 1988).

Abstract

Myotyphlus jansoni (Matthews, 1878), a rare and the only rove beetle species from the subtribe Amblyopinina in Australia that occurs in the fur of small mammals, is revised. Male genitalia have been examined for this species and, as a result, it is divided into three species: *M. jansoni* restricted to Tasmania; as well as *M. newtoni* **sp. nov.** and *M. wurra* **sp. nov.** described as new from mainland south-western Australia. Distribution, bionomics and host associations are summarized for all three species with a conclusion that at least *M. newtoni* sp. nov. and *M. wurra* sp. nov., in addition to the mammal-associated records, also occur in bat guano in caves, or on the ground. Neither of three *Myotyphlus* species is specific for a particular mammal species, and the genus as a whole occurs on several species of *Rattus*, on *Pseudomys higginsi*, and on *Antechinus swainsonii*. Presumably *Myotyphlus* is not as strongly associated with the host mammals as the more diverse American mammal-associated genera of Amblyopinina. Ecology and putative sister-group relationships of *Myotyphlus* reviewed in the broad context of mammal-rove beetle mutualism suggest an independent origin of this mammal-associated lifestyle in the Neotropics and Australia from different free living lineages of Amblyopinina.

Key words: systematics, Staphylinini, Amblyopinina, Australia, Neotropical, new species

1. Introduction

Insects and mammals are two very different, diverse, and evolutionarily successful animal groups dominating all habitable landscapes on our planet. They are mutually dependent on each other as valuable components of terrestrial ecosystems through indirect associations, for

example insects as pollinators of plants and grazing mammals as plant consumers, or dung beetles as coprophages and mammals as dung producers. These balanced biotic interactions between two animal classes are crucial for the biosphere and yield important benefits for humans. At the same time direct interactions between insects and mammals mostly appear antagonistic. For example, many mammals predate on insects, or some insects consume mammal blood or otherwise utilize them as hosts during parasitism. In fact with about 6000 species of ectoparasitic insects (Marshall 1981), their parasitism on mammals is the main type of direct relationships between these animal classes followed by mammal predation on insects.

On the contrary, there seems to be hardly any examples of an insect-mammal mutualism. This is quite remarkable since mutualisms, defined as interactions that benefit both parties involved, are frequently encountered in the natural world (e.g. Boucher *et al.* 1982; Herre *et al.* 1999; Weiblen & Treiber 2015). One example of an insect-mammal direct association interpreted as mutualism is the interaction between sloths and pyralid moths that, however, also involve the third agent, the algae in Central America (Pauli *et al.* 2014). A much more straightforward case of insects truly mutualistic to mammals has been discovered earlier (Ashe & Timm 1987a) among Amblyopinina, a subtribe of rove beetles (Staphylinidae) that are a mega-diverse, globally distributed beetle family. In fact, the peculiar looking Amblyopinina rove beetles from the Neotropical region were known to entomologists for more than a century who gradually described their 6 genera (*Amblyopinus* Solsky, 1875, *Edrabius* Fauvel, 1900, *Amblyopinoidea* Seevers, 1955, *Megamblyopinus* Seevers, 1955 and *Chilamblyopinus* Ashe & Timm, 1988 from South America, and *Myotyphlus* Fauvel, 1883 from Australia), altogether comprising 65 species (Herman 2001). But due to these strange looking beetles (Fig. 1) repeatedly being collected in the fur of live small mammals, mostly rodents, and reminiscent of fleas, they were always presumed to be ectoparasites on their mammal hosts. Seevers (1955), however, had noted that the hosts were ‘insensible’ to the beetles on their bodies, even if the beetles were crossing the hosts’ eyes. Later, Ashe and Timm (1987a) extended Seevers' (1955) observation into an interesting experiment. They took live specimens of *Amblyopinus tiptoni* Barrera, 1966 and placed them on the mouse *Scotinomys teguine* (Alston, 1877) that is not a host of the beetle but one that is similar in fur type and body size to its natural hosts. The mice reacted by actively grooming the beetles out and exterminating them, such behavior suggesting a significant degree of coadaptation among beetles and their natural hosts required in case of mutualism. Additionally, they observed the beetles feeding on the ‘real’ ectoparasites of their hosts, such

as fleas or mites. Ashe and Timm (1987a) argued that as predatory rove beetles Amblyopinina became adapted to hunt true mammal ectoparasites directly from the fur of their hosts. In return, the hosts evolved high tolerance to the beetles on their bodies. Therefore, these rove beetles and their mammal host display a highly specialized case of mutualism.

In spite of the recent papers by Ashe and Timm (1987a, b) which gave a good summary and a novel look at the amblyopinine biology, this rare and perhaps the only known example of an insect-mammal mutualism, was not placed in the spotlight of the broader evolutionary research. One reason for that is lack of a sound phylogenetic study of Amblyopinina resulting in confusing definition of these rove beetles and their putative sister relationships. Secondly, poor outreach of the specialized sections of systematic entomology to other biological disciplines acted as an impediment for making these beetles accessible for studies outside that field. Recently a series of phylogenetic studies of Staphylinini (Solodovnikov 2006; Solodovnikov & Schomann 2009; Chatzimanolis *et al.* 2010; Brunke *et al.* 2015) finally defined a broader monophyletic group that gave rise to these mammal mutualistic amblyopinines. These studies, however, did not address one of the core evolutionary questions about this mutualism: whether all mammal associated Amblyopinina stem from a single free living ancestor, or whether they are in fact polyphyletic. In other words, it remains open if this very unique case of mutualism among insects and mammals has a single origin or arose multiple times from closely related free living ancestors within the rove beetle subtribe Amblyopinina. *Myotyphlus jansoni* (Matthews, 1878), the only Australian representative of the otherwise South and Central American mutualistic amblyopinines is the key taxon for seeking answers for this question. In addition to its geographic distribution as an outlier, morphology of that species is not as derived as in species of the main (Neotropical) mammal-associated stock of Amblyopinina. And the ecology of its association with mammals, as far as known (Hamilton-Smith & Adams 1966) seems less strict than in the Neotropical species. Although being a truly unique beetle in Australia critical for understanding the rare biological phenomenon of insect-mammal mutualism, *M. jansoni* remains a very poorly known species without a proper modern taxonomic treatment. Even its aedeagus, for example, has never been dissected and studied, although illustrating this structure is now a standard in species diagnostics of rove beetles, especially Staphylinini. To fill all abovementioned gaps, here we target the systematic revision of *M. jansoni* and summarize all available data about its distribution, bionomics and biology. We discuss these data in the phylogenetic context elucidating the origin of the unique example of insect-mammal mutualism displayed by rove beetles. Morphology of *M. jansoni* had to be revisited since none of the previous descriptions

accounted for systematically important characters that have been introduced in the latest phylogenetic work on Staphylinini. Morphology is particularly important in this case as hosts and/or symbionts frequently evolve novel characters or lose them (Herre *et al.* 1999). With the closer examination of this amazing living species of the Australian continent, we have discovered that in fact it consists of three species two of which are new to science and are described here. Due to the paucity of the available material, our knowledge of the distribution and biology of this species complex remains limited, while its species discrimination is possible only with the examination of male genitalia. But we hope that this paper will stimulate further study of this species complex, also by DNA-based methods and with biological observations. By reviewing mammal-associated mutualism in beetles and insects in general here, we also aim to bridge the gap between technical systematics of Amblyopinina and broader evolutionary research of this group, potentially manifesting the multiple origin of a remarkable and unique case of mutualism between insects and mammals.

2. Materials and methods

Beetles were examined using a Leica MZ APO dissection microscope. They were studied as either dry pinned material or as wet specimens in petri dishes containing glycerin. Dissected genitalia are stored in glycerin in vials or mounted in water soluble transparent Lompe solution on see-through cards, those attached to an insect pin beneath respective specimens. Measurements were taken using an ocular micrometer and are given in millimeters (mm). Morphological characters are abbreviated as follows FL = Forebody Length (posterior margin of elytra to anterior margin of labrum), HL = Head Length (from apex of labrum to neck constriction), HW= Head Width at widest point, HL*HW= Head Length X Head Width. Specimen label data is repeated verbatim, one forward slash (/) indicates separation of labels. This paper is based on the study of specimens from the following collections:

BMNH – Natural History Museum, London (R. Booth, M. Barclay)

CSIRO - Australian National Insect Collection Canberra (C. Lemann)

FMNH - Field Museum of Natural History, Chicago (J. Boone, C. Maier)

SAM - South Australian Museum, Adelaide (P. Hudson)

ZMUC – Zoological Museum at the University of Copenhagen (part of the Natural History Museum of Denmark (A. Solodovnikov, S. Selvantharan)

Habitus photographs were taken using either the Visionary Digital Imaging Systems with a Canon EOS 7D (*Myotyphlus jansoni* habitus) or a Leica MZ 16 A dissection scope combined with a Leica DFC450 C camera (habitus images in Fig. 1) and stacked using Zerene Stacker software. A middle leg was taken from *M. jansoni*, mounted on aluminium stubs, coated with platinum/palladium and studied in a JEOL JSM-6335F scanning electron microscope. The distribution map was created using QGIS 2.12 Lyon and the Natural Earth Free vector and raster map data (naturalearthdata.com). The schematic phylogeny (Fig. 1) was drawn in Adobe Illustrator CS6. The graph (Fig. 2A) was made using R studio 3.2.3 using the package ‘ggplot2’. Male genitalia were digitally inked from photos using Adobe Illustrator CS6.

3. Systematics of the genus *Myotyphlus*

3.1. Taxonomic history

Until present the genus *Myotyphlus* was known from a single species *Myotyphlus jansoni* (Matthews, 1878). That species was described in the genus *Amblyopinus*, at that time associated with the rove beetle subfamily Tachyporinae. Its original description (Matthews 1878) was based on two specimens collected in Tasmania. The description was very careful and even contained illustrations of morphological details which was rare at that time. Fauvel (1883), who studied this species shortly after, argued that it must be moved from *Amblyopinus* to its own genus that he named *Myotyphlus*. Matthews (1884) agreed with the separate generic status of this species, but he did not like Fauvel’s name *Myotyphlus* and proposed the genus name *Cryptommatus* instead. Contrary to Fauvel (1883) who erected *Myotyphlus* without elaborate character assessment or even a genus description, Matthews’ (1884) description of *Cryptommatus* was very detailed. Also Matthews (1878, 1884) pointed to the affinity of *Myotyphlus jansoni* with the genus *Philonthus*, i.e. towards the subfamily Staphylininae where *Myotyphlus* currently belongs. Naturally, Matthews’ genus *Cryptommatus* was placed in synonymy with *Myotyphlus* in accordance with the rules of zoological nomenclature. Apart from several catalogues and ecological faunistic records (Lea 1925; Hamilton-Smith & Adams 1966), *Myotyphlus jansoni* was redescribed, illustrated and compared to the American members of the group only several decades later, in the monograph of Seevers (1955). Later, the species was mentioned in Machado-Allison (1963), Newton (1985), and Ashe & Timm (1988) who expressed opinions on its possible phylogenetic affinities that we address in the discussion.

3.2. Recognition of the genus

Among all rove beetles of Australia *Myotyphlus* is easily recognized based on the following features of its habitus (Fig. 2D): overall depigmented body; characteristically trapezoidal head noticeably widened posteriorly and with very reduced eyes situated anteriorly on the head; reduced elytra that are slightly shorter than the pronotum; and a black comb on the first mesotarsomere in both sexes (Fig. 3). Additional characters such as the quadrate pronotum; apical segment of labial and maxillary palpi about half the length of the penultimate segment; lack of post-coxal process on the strongly deflexed hypomera; and presence of sub-basal carina connecting spiracles on abdominal tergites III to V are important to note for placing *M. jansoni* in its proper lineage within Amblyopinina (for more details see below). Among Australian Staphylinidae *Myotyphlus* may superficially appear similar to *Quedius mediofuscus* Lea, 1910.

3.3. *Myotyphlus jansoni*, revised concept

Type material examined: Australia: Tasmania: syntypes: 2 males, 1 female, ‘Tasmania A. Simson // 3137’ (SAM).

Other material: Australia: Tasmania: 2 females, ‘3137 *Cryptommatus jansoni* Matth Tasmania (SAM); 1 female, ‘From bush rat [something illegible] Tas. H.M. Nicholls/ J. 12506 *Cryptommatus jansoni* Matth. Tasmania base of rats tail cotype’; 2 females with same geographic labels but without determination label; (SAM); 1 male, 1 female: ‘Cradle Mt, 6.xii.1964, R.H Green/ *Pseudomys higginsii*/ *Myotyphlus* >3 spp. (2+ new) det. A. Newton 1981’. 2 males: ‘Franklin River, below Gordons Peak, 15 Jan. 1983, E.B Britton’. 1 male, 1 female: ‘Mt Kate, 16.x.1964, R.H Green/ *Rattus lutreolus*’. 1 female: ‘Florentine Valley, 7.vii.1959, B.C Mollison/ *Rattus lutreolus valentinus*’. 1 female: ‘Corinna, 8.ii.1965, R.H Green/ *Antechinus swainsonii*’. 1 female: ‘Tasmania/ *Myotyphlus jansoni* Matth./ 296 [in red]/ M. Cameron Bequest B.M. 1955-147’ (BMNH).

Redescription

Measurements: FL (2.6-2.8), HL (0.7-0.8), HW (0.95-1.1), HL*HW (0.665-0.88).

Overall pale brown, not strongly pigmented beetles with highly reduced eyes, a distinctive trapezoid shaped head and black combs on the first mesotarsomere in both sexes (best viewed

from a lateral angle, Fig. 3). Habitus as in Fig. 2D.

Head trapezoidal, posteriorly widened, with fully developed neck constriction. Nuchal ridge developed laterally, absent dorsally. Eyes consisting of few ommatidia and therefore extremely small, positioned anteriorly very close to base of mandibles. Gular sutures slightly diverging anteriorly. Postmandibular ridge present. Postgenal ridge weakly developed, sinuate, projecting anteriorly and connecting the gular suture and infraorbital ridge. Infraorbital ridge short, extending just past the post-genal ridge. Anterior area of gula with pair of setae. Apical segment of labial and maxillary palpi aciculate, about half the length of penultimate segments. Labrum short and bilobed with translucent membrane bearing setae. Mandibles with long and distinct dorsal groove. Dorsal and ventral sides of head with distinct transversal microsculpture. Temples with scattered setae in addition to macro setae. Antennae rather short; first antennomere about as long as antennomeres 2 and 3 combined. Antennomeres 1–3 only with setae; antennomeres 4–11 with tomentose pubescence and setae. Pronotum quadrate (sometimes slightly transverse) with one pair of shallow punctures in each dorsal row and sparse micropunctures covering pronotum (visible under adequate light and magnification). Pronotal hypomera strongly deflexed and thus not visible in lateral view. Pronotum without translucent postcoxal process. Basisternum with pair of macro setae. Elytra shorter than pronotum, with even but sparse punctation. Scutellum only with one (anterior) scutellar ridge. Humeral angles of elytra with several spines. Hind wings absent entirely. Mesosternal process obtuse, rounded. Metasternal process notched. Legs concolorous with body. Tarsal formula 5-5-5. Both sexes with protarsi moderately dilated with white adhesive setation ventrally. Both sexes with the first tarsomere of the mesotarsus bearing a black comb (Fig. 3). Fifth tarsal segment with a pair of empodial setae. Mesocoxae larger than metacoxae. Metacoxae with transverse carina. Abdomen moderately dorsoventrally flattened. Tergites III to V with sub-basal carinae connecting spiracles. Male sternite VIII with apical median incision. Protergal glands (hidden under elytra) positioned anteriorly, manifested as an oval impression bordered by small setae.

Male. Aedeagus with paramere closely attached to median lobe, apex of paramere in dorsal or ventral view very blunt (Fig. 2B).

Distribution

Based on new data from specimens examined here and earlier records (Hamilton-Smith & Adams 1966), *M. jansoni* has been recorded from several isolated localities in Tasmania (Fig. 2C, Table 1). Earlier records of *M. jansoni* for Victoria and New South Wales (Hamilton-

Smith & Adams 1966) in fact probably belong to the new species described below, but study of those specimens and male genitalia is required to clarify their identity.

Bionomics

According to the specimen label data available to us, *M. jansoni* has been recorded from the following mammals in Tasmania: from *Rattus lutreolus*, *R. velutinus*, *Pseudomys higginsii* and *Antechinus swainsonii* (Table 1). The only available information about the two specimens of *M. jansoni* studied by Matthews (1878) is that they were received by Mr. Janson in 1877 from Mr. Simson among other Coleoptera collected in Gould's Country, Tasmania. Bionomic records associated with both specimens indicated that they were collected 'in the fur of a living rat'. Fauvel (1883) mentioned that he had studied *M. jansoni* based on the same Tasmanian material from Mr. Simson and an additional specimen found in Brussels museum. He did not mention any biological information about the species other than published in Matthews (1878). The second contribution to the study of this species by Matthews (1884) was based on the same material as its original description. In the summary on parasitic beetles, Kolbe (1911) similarly to South American amblyopinines, listed *M. jansoni* as a mammal ectoparasite, solely based on the information earlier published about that species in Matthews (1878, 1884). Lea (1925) listed nine specimens of *M. jansoni* (as *Cryptommatus jansoni*) that 'were all taken clinging to the anal hairs of bush rats [modern perception of 'bush rats' seems to refer to *Rattus fuscipes*], in Tasmania, by Messrs. Aug. Simson and H.M. Nichols, and in Victoria by Mr. E. Jarvis'. With new species concepts based on male genitalia, Lea's (1925) records from Victoria correspond not to *M. jansoni* but to either *M. newtoni* or *M. wurra*. As far as the Tasmanian material of real *M. jansoni* is concerned, clearly the specimens mentioned by Lea (1925) were additional to the type material, confirming both its rat-associated biology. In his revision of Amblyopinina, Seever (1955) based his treatment of *Myotyphlus* on the previously published data, and he assumed that the host of *M. jansoni* must be 'the house rat as there are no native Tasmanian rodents'.

Comparison

Myotyphlus jansoni differs from its two newly described congeners (see below) only in the shape of the aedeagus: its paramere apex is distinctly more blunt than either *M. newtoni* or *M. wurra*, and therefore looking somewhat truncate (Fig. 2B). Based on the available males that can be assigned to species, *M. jansoni* is larger than the largest specimens of *M. newtoni*. On Tasmania *Myotyphlus jansoni* is the only species of the genus.

3.4 *Myotyphlus newtoni* sp. nov.

Holotype: Australia: *Victoria*: 1 male, ‘Victoria, French Island, 29.viii.1967, R.M. Warneke’/’*Rattus fuscipes assimilis*’. (CSIRO)

Paratypes: Australia: *Victoria*: 2 males: ‘Olson’s Bridge, 11.ix.1959, R.M Warneke/ *Rattus assimilis*’ (CSIRO). 1 female: ‘French Island, 29.viii.1967, R.M Warneke/ *Rattus fuscipes assimilis*’ (CSIRO). 1 male: ‘Loch Valley, in fur of *Rattus assimilis*, 27.vii.63, R.M Warneke/ *Myotyphlus jansoni* det. Seevers’ (CSIRO). 1 male, 1 female: ‘Bat’s Ridge, 20.i.1968, J.H Seebeck/ *Rattus fuscipes grayii*’ (CSIRO). **New South Wales**: 1 male: ‘Deua NP NSW, Deua Cave, 5 Apr. 1986, E. Holm, ex. Bat guano/ *Myotyphlus* sp. Det. J.F. Lawrence’ (CSIRO).

Description

Measurements: FL (1.5-2.4), HL (0.6-0.9), HW (0.6-0.9), HL*HW (0.36-0.81)

Externally the new species is the same as *M. jansoni*, but on average smaller. The smallest specimens of *M. newtoni* are significantly smaller than *M. jansoni* (Fig. 2A). *Myotyphlus newtoni* has very characteristic acute apex of the paramere (Fig. 2B), that easily distinguishes this species from either *M. jansoni* or *M. wurra*.

Etymology

We are pleased to dedicate the new species to Alfred Newton, who invested significant time and effort in the study of Australian Staphylinidae. In particular, he has examined some of the material we used in this paper, and based on his notes we could see that he also thought that ‘*M. jansoni*’ maybe a complex of several species.

Distribution

Presumably *M. newtoni* is broadly distributed in South-Eastern Australia. Reliable male-associated records stretch from Bat’s Ridge in the west to Deua Cave in the east (Fig. 2C, Table 1).

Bionomics

According to the specimen label data available to us, *M. newtoni* has been collected in the usual ground surface habitats of various localities, and in Deua Cave in New South Wales. In the ground surface habitats, it was recorded from *Rattus fuscipes*, *R. assimilis*, and *R. grayii*.

In the Deua Cave a single male was collected not from rats but in the layer of bat guano. Significant material reported as '*M. jansoni*' in Hamilton-Smith and Adams (1966) from *Miniopterus schreibergsi* (Kuhl) bat guano in Lake Gilleard Guano Cave near Warnambool, Victoria, and in a cave within the Southern Limestone at Jenolan, New South Wales apparently can be attributed to *M. newtoni* based on the distribution. Interestingly, that Hamilton-Smith and Adams (1966) also reported a personal communication of R.M. Warnecke of the Victorian Fisheries and Wildlife Department who had found '*M. jansoni*' (presumably *M. newtoni*) on only three of the 2000 examined *Rattus assimilis*. Among beetles found on these three rats, some were found on scrotum of one rat, and all other were confined to the area immediately surrounding the anus of the host animal. All beetles were attached to rats by the feet only without any signs of skin disorders on host rats. Hamilton-Smith and Adams (1966) stressed that larva of '*M. jansoni*' has never been found anywhere. Based on new findings, they overall concluded that this species is not an obligate parasite of mammals as in Neotropical amblyopinines, but maybe the case of an initial evolutionary step from a free-living lifestyle to ectoparasitism. Although we have examined a number of specimens collected by R.M. Warnecke, it is not clear if any of them are related to the personal communication between R.M. Warnecke and Hamilton-Smith and Adams (1966).

3.5 *Myotyphlus wurra* sp. nov.

***Holotype:* Australia: Victoria: 1 male, 'Olson's Bridge, 11-9-59 (Sept), R.M. Warnecke, *Rattus assimilis*' [specimen mounted from alcohol, label handwritten by JJS]. (CSIRO).**

***Paratypes:* Australia: Victoria: 4 males: details as for holotype. (CSIRO).**

Description

Measurements: FL (2.2-2.7), HL (0.8-1), HW (0.8-1), HL*HW (0.64-1).

Externally the new species is the same as *M. jansoni* or *M. newtoni*, but differs from both of them in a characteristically rounded apex of the paramere (Fig. 2B). In body size *M. wurra* greatly overlaps with *M. jansoni* and some larger specimens of *M. newtoni*.

Etymology

The species epithet refers to the aboriginal word for ‘rat’ or ‘common rat’, from which all known specimens of *M. wurra* were collected. The species name ‘wurra’ is a noun in apposition.

Distribution

So far *Myotyphlus wurra* is known only from the type locality, Olson’s Bridge in Victoria (Fig. 2C), where it occurs sympatrically with *M. newtoni*.

Bionomics

The new species was collected on *Rattus assimilis* and is only known from the type locality.

3.6 *Myotyphlus* sp.

The following specimens refer to females which were collected from Olson’s Bridge, Victoria where *M. newtoni* and *M. wurra* occur sympatrically and therefore female cannot be assigned to species. The specimen from New South Wales refers to a female collected without association with males. Female only specimen records from Tasmania are presumed to be *M. jansoni* since that is the only known species from Tasmania.

Material examined: Australia: Victoria: 3 females, ‘Olson’s Bridge, 11.ix.1959, R.M Warneke/ *Rattus assimilis*’ (CSIRO). **New South Wales:** 1 female, ‘South Ramshead, 1850m Kosciusko Nat. Pk. NSW, May 1981, Ken Green, pitfalls/ A.N.I.C Coleoptera, Voucher No. 83-0058’. (CSIRO).

4. Discussion

4.1 *Myotyphlus jansoni*: how many species?

Observed variation in the shape of the aedeagus suggested that ‘*M. jansoni*’ is a complex of at least three species where, based on the identity of the type material, true *M. jansoni* is confined to Tasmania only. Strong geographic isolation of Tasmania, combined with the noticeable difference in the shape of aedeagus between *M. jansoni* and two new species from the mainland Australia, speaks for the lacking gene flow between the Tasmanian and the mainland populations. Sympatric occurrence of *M. wurra* and *M. newtoni* and lacking

transitional states between their respective aedeagi shapes suggest their genetic isolation from each other and thus separate species status even though we did not find difference between these species in external characters. Additional material from throughout the genus range would help resolve its taxonomy more rigorously using morphology and DNA based markers. Combined with its unique biology and occurrence in caves, there may be complex microevolutionary processes that take place in this species complex, with a possibility that new material may reveal more new species.

4.2 Sister group relationships and biogeography of *Myotyphlus*

Seevers (1955) expressed an idea that *Myotyphlus* was the basal Amblyopinini connecting them to related tribe Quediini. He proposed the affinity of *Myotyphlus* with the South American *Edrabius* based on a single character – the highly reduced eyes located close behind the antennal insertions. As Quediini were known mostly as a Northern Hemisphere group, Seevers (1955) proposed a complex hypothesis of the northern origin of Amblyopinini from Quediini ancestors and their dispersal from North to South America together with mammals during great faunal exchange between both continents. Therefore, basal nature of the Australian *Myotyphlus* and its affiliation with *Edrabius* was a perplexing fact for Seevers' hypothesis, which he could not explain. Machado-Allison (1963) also argued that *Myotyphlus* could be closely related to the South American genus *Edrabius*, but, contrary to Seevers (1955), he suggested a southern origin of Amblyopinini. Bringing new biological observations for *M. jansoni*, Hamilton-Smith and Adams (1966) also mentioned that it was apparently closely allied to the Neotropical amblyopinine genus *Edrabius*. Largely based on their finding that *Myotyphlus* was not as strictly associated with rats as it was thought before, they suggested that it may have to be moved from Amblyopinini to Quediini. Newton (1985) was the first who raised the possibility that *Myotyphlus* may be derived from the free-living 'quediines' of Australia, independently of the genera found in the Neotropical region which would result in a polyphyletic origin of this mammal-associated group. Ashe and Timm (1988) recognized a few lineages among mammal-associated amblyopinines: Chilean *Chilamblyopinus* as a very basal lineage; South-Central American genera *Amblyopinodes*, *Amblyopinus* and *Megamblyopinus* as a more derived lineage; and *Edrabius* and *Myotyphlus* as two isolated lineages of unclear sister-group relationships, not necessarily related to each other (Fig.1). They emphasized the more ecologically generalized *Myotyphlus* as a very

important taxon for testing the monophyly of the mammal-associated amblyopinines. Based on the presence of tarsal combs in *Myotyphlus* and some Australian Quediini (unique feature among Staphylinini), Ashe and Timm (1988) agreed with Newton (1985) that the former may be more closely related to the latter than to other (Neotropical) Amblyopinini.

Much uncertainty and controversy about sister-group relationships for *Myotyphlus* and other amblyopinines came from the very poor state of knowledge of the ‘Southern Hemisphere quediines’ and the fact that Seevers (1955), Machado-Allison (1963), Ashe and Timm (1988) or others thought that their putative sister group had to be sought within the bipolar global subtribe Quediina. Since then systematics of Staphylinini has changed significantly. In particular, it was shown that ‘north temperate’ and ‘south temperate’ ‘Quediina’ are non-related lineages (Solodovnikov 2006; Solodovnikov & Schomann 2009; Chatzimanolis *et al.* 2010; Brunke *et al.* 2015). The former became a subtribe Quediina in a restricted sense, while the latter became a subtribe of its own that received the name Amblyopinina since it included the name bearing genus *Amblyopinus* Solsky, 1875 and other mammal associated genera (*Amblyopinoides* Seevers, 1955, *Chilamblyopinus* Ashe & Timm, 1988, *Edrabius* Fauvel, 1900, *Megamblyopinus* Seevers, 1955 from South America and *Myotyphlus* Fauvel, 1883 from Australia). Internal phylogeny of Amblyopinina in that new sense, however, remains unknown and currently impossible to reconstruct because of the very poor state of the alpha-taxonomic knowledge of the numerous free living members of this subtribe. Our work in progress suggests that free living amblyopinines comprise the following major lineages: *Loncovilius*-lineage for species with enlarged middle and hind tarsi; *Natalignathus*-*Atanygnathus*-lineage with elongated mouthparts; *Heterothops*-lineage with fully fused paramere and median lobe of the aedeagus; *Cheilocolpus*-*Rolla*-*Philonthellus*-lineage with species characterized by short ‘infraorbital ridges’, absent translucent post coxal process, wide anterior tarsi, often narrow or aciculate apical segment of maxillary palps and two basal carinae on abdominal segments III-V; a lineage consisting of one-two new genera to be described with fully developed ‘infraorbital ridges’, narrow anterior tarsi, absent translucent post coxal process and two basal carinae on abdominal segments III-V; *Quediopsis*-lineage with securiform last segment of maxillary palps; and *Sphingoquedi*-*Quediomimus*-*Mimosticus*-*Ctenandropus*- lineage with species bearing black iridescent combs. Such combs are unique among Staphylinini (and Staphylinidae) and, in different species or genera, they can be located on the first mesotarsomere, mesotrochanter, mesofemora, or metacoxae, respectively. Often these combs are present only in males, but those on mesotarsomeres may be developed in both sexes. Except the strictly South American

Loncovilius-lineage, South African (*Natalignathus*) and wide-spread (*Atanygnathus*) lineage and wide-spread *Heterothops*-lineage, all other lineages have disjunct distributions across several Gondwana-derived landmasses (mainly South America, Australia, New Zealand, New Caledonia and New Guinea) where they form major to notable share of the entire Staphylinini fauna. Amblyopinina are notably absent or very poorly represented in India, Madagascar and Africa, i.e. the Gondwana-derived landmasses that got separated earlier. Such distribution pattern hints that Amblyopinina is a relatively old lineage of Staphylinini whose major lineages evolved during Cretaceous - Early Tertiary when at least South America, Australia and New Zealand were connected via Antractica. Except the *Loncovilius*-lineage, all other amblyopinine lineages occur in Australia. Based on the presence of combs and characters of *Myotyphlus*, it can be assigned to *Sphingoquedius*-*Quedimimus*-*Mimosticus*-*Ctenandropus* lineage where the majority of the Australian Amblyopinina belong (e.g., '*Quedius*' *bellus* Lea, 1925, '*Quedius*' *cordatus* Lea, 1925, *Quedius lateroflavus* Lea, 1925, *Quedius metallicus* Fauvel, 1878 and many other species still formally remaining in the genus *Quedius*). Noteworthy that the black combs are absent in all genera of the truly mammal-mutualistic genera of the Neotropical region even though there are free living comb-bearing species Amblyopinina there. All these observations suggest that *Myotyphlus* stems from a lineage different from the one(s) that gave rise to South American mammal mutualistic mammals.

4.3 *Myotyphlus* association with Australian mammals, historical perspective

According to the available data, all species of *Myotyphlus* are known only as adults that have been recorded. *Myotyphlus jansonii* was found on rodents (*Rattus* spp. and *Pseudomys higginsi*) and on *Antechinus swainsonii*, a species of carnivorous dasyurid marsupial *Myotyphlus newtoni* and *M. wurra* were found only on *Rattus* spp., and, at least on two occasions they were collected not from mammals but in caves from under the surface of bat guano. Finally, one female specimen identified as *M. newtoni* based on the distribution was collected in a pitfall trap in the usual above ground microhabitat at high elevation of Mt. Kostiusko. Therefore, it seems that none of *Myotyphlus* species has strict association with any particular host mammal species. Probably, beetles do not even stay on the mammal body all the time, or even some populations, for example those found in bat guano, do not occur on mammals at all. Presumably, larvae of the species develop outside the mammal host body.

The strength of the association between *Myotyphlus* and caves, is also unknown. Presumably, the mammals which the *Myotyphlus* specimens were taken from, have been trapped in the usual above ground habitats. But it may well be that mammals with beetles also occur in caves, at least episodically. It is also unclear whether a specialized depigmented and small-eyed habitus of *Myotyphlus* was a primary adaptation for subterranean biology where beetles and mammals could come in contact, or the association with mammals came first, followed by adaptations to cave microhabitats. In any case, specialized biology and associated morphological adaptations of *Myotyphlus* seem to be a relatively young phenomenon in the evolutionary history of Australian Amblyopinina given the time estimates derived from the study of the evolutionary history of their hosts in Australia.

Since amblyopinines must have been present in Australia for tens of millions of years, it is quite noteworthy that in spite of rich ancient indigenous and diverse fauna of marsupials in Australia, the only marsupial that *Myotyphlus* has been recorded from, is the carnivorous marsupial genus *Antechinus* (Dasyuridae). It is comprised of 12 species distributed in Australia and New Guinea (Flannery 1995; Strahan 1995; Armstrong *et al.* 1998) with the genera from those two regions forming two monophyletic lineages (Armstrong *et al.* 1998). In that study, Armstrong *et al.* (1998) made no biogeographic inference from their phylogeny, however like rodents dasyurids also appear to be a recent group in Australia (Crowther & Blacket 2003), with the oldest fossil that can be placed in an extant genus dated at around 4.5 mya (early Pliocene). More recently it has been suggested that extant Dasyuridae have earlier origins in Australia with *Antechinus* originating around 11.9 (9.5–14.5) mya (Woolley *et al.* 2015).

The first group of rodents that reached Australia from Asia most likely via New Guinea were the *Pseudomys*-group of rodents (Muridae), with one genus and species recorded as a host of *M. jansoni* (*Pseudomys higginsi*) (Simpson 1961). This pattern of colonization of Australia from Asia via New Guinea has been found in a number of studies on different organisms and can be explained by the close geographic affinity of Australia and New Guinea and frequent land connections between those during the Pliocene. The diversity of native *Rattus* (Muridae) species is the highest in New Guinea and followed by Australia, mainland south-east Asia and Sulawesi (Aplin *et al.* 2003). Molecular phylogenetic dating and the earliest of Australian murine fossils suggest that diversification of the native Australian rodents began between 5.1 and 5.5 mya (Rowe *et al.* 2008). Based on mitochondrial genome data, Robins *et al.* (2011) proposed that *Rattus fuscipes* and *R. lutreolus* (recorded as *Myotyphlus* hosts) are among the oldest lineages of Australian rats and not part of the

colonization from New Guinea, but rather share a common ancestor with *Rattus* that colonized Australia out of New Guinea. In that paper they also suggested recent interchanges between the Australian and New Guinean *Rattus* fauna during the Pleistocene, supporting previous morphology-based analysis (Taylor *et al.* 1983). Finally, it is interesting to note that *Rattus rattus* and *Rattus norvegicus* were introduced to Australia by Europeans and there are no records of *Myotyphlus* from those species.

For comparison, hosts of the more diverse American symbiotic amblyopinines represented by many more different mammal species, almost equally split between marsupials and rodents (Seevers 1944, 1955). The earliest fossil marsupials in South America are dated to 61-65mya. The marsupial genera *Didelphis*, *Metachirus* and *Monodelphis* from which American symbiotic amblyopinines have been recorded, are part of a clade that originated during the early Eocene (ca.51 mya), based on semi-parametric divergence dating methods which relax the molecular clock (Nilsson *et al.* 2004). Those amblyopinines are also recorded from *Rhyncholestes*, a genus sister to *Caenolestes* (Meredith *et al.* 2008) and Palma & Spotorno 1999). Nilsson *et al.* (2004) suggested a divergence time between those two sister genera of around 30 mya, during the Oligocene.

Hystricomorpha, a suborder of rodents and recorded host of South American Amblyopinina have been suggested to have Oligocene (23-34mya) origins in South America, although the exact source of their South American fauna seems to still be controversial (Huchon & Douzery 2001; Upham & Patterson 2012). According to Smith and Patton (1999), the ancestor of the rodent subfamily Sigmodontinae from which many mammal-mutualistic Amblyopinina have been collected, dispersed to South America from North America across the water barrier, probably during the Miocene. The earliest recognized fossils of the Sigmodontinae from Argentina dated at about 4-5 mya (early Pliocene) are consistent with that hypothesis (Pardiñas & Tonni 1998). There are variations on each of the two hypotheses mentioned above, but it is not within the scope of this paper to discuss them in detail, but rather we aim to draw attention to the controversy and potential temporal variation in the colonization and radiation of Amblyopinina hosts in South America. It is apparent that American symbiotic Amblyopinina are adapted to mammals that had much earlier origins (particularly the marsupials), but also more recent rodent lineages.

Lower degree of morphological specialization, frequency of records outside mammal bodies, and relatively short period of time available for possible co-evolution with their hosts, suggest

that *Myotyphlus* may not be as strong case of mutualism with mammals as manifested by South American genera.

4.4 *Myotyphlus* as an early stage of insect-mammal mutualism and other other examples of mammal-insect

The case of *Myotyphlus*, that possibly displays an early stage of the evolution towards more refined mutualism, reveals a certain gradient within such insect-mammal interactions, and it draws our attention to other rare cases of similarly looking relationships. When Popham (1962) reported the presumably ectoparasitic earwig *Arixenia esau* Jordon, 1909 (Dermaptera) feeding on the skin of *Cheiromeles*, he noted that another species of the same genus, *A. jacobsoni* Burr, 1912 with less specialized mouthparts, feeds on insects found in bat guano. Later, Marshall (1972) suggested the interaction between *Arixenia* earwigs and *Cheiromeles* bats to be a mutualism where earwig feeding mode keep the bat body clean. Waage (1979) further discussed the relationship between *Arixenia* and its bat hosts and described it as a commensalism with the potential of actually being a mutualism if a sanitary benefit to the bat can be attributed to the feeding strategy of *Arixenia*. Noteworthy is that even though rove beetles and earwigs are members of phylogenetically remote insect orders, convergently they represent very similar adaptive types, with flexible elongate body and short elytra.

Another example is phylogenetically close to rove beetles since it concerns a derived staphylinoid beetle *Platypsyllus castoris* Ritsema, 1869 from the family Leiodidae. *Platypsyllus castoris* is believed to be an ectoparasitic beetle specialized on Old and New world beavers (Peck 2006) based on observations of its larvae consuming the epidermal tissue of beavers as well as skin secretions and wood exudates (Wood 1965). In view of the Amblyopinina and earwig examples, it would therefore appear that this relationship also has the potential to be a mutualism, if evidence can be attained of any sanitary (or other) benefit to the beaver.

Finally, the last example of insect-mammal mutualism involves Lepidoptera. Initially it was described as phoresis between *Cryptoses* moths and a species of three-toed sloth (Waage & Montgomery 1976) where moths require the relationship but they pose no consequence (positive or negative) on the sloth. Adult female moths that occur in the fur of sloths disembark their host during its descent to the forest floor for defecation. Female moths oviposit on the fresh dung of their host sloth where development of the moth next generation

takes place until newly hatched moth adults disperse into the forest canopy and find sloths again. The relationship between moths and sloths started to be seen as mutualism only recently after Pauli *et al.* (2014) added a third organismal type (algae *Trichophilus sp.*) in the system. They found that sloths with algae-infested fur consume their algae via self-grooming and apparently benefit from adding algae in their diet, while moths, presumably, facilitate the increase of algal biomass in the sloth's fur. In turn, by descending for defecation to the ground, the sloths facilitate moth's life cycle. However, the exact mechanism driving the positive relationship between moth density and algal biomass remains speculative, and therefore this entire complex case of presumed mutualism is not fully understood yet.

5. Conclusions

The Staphylinini subtribe Amblyopinina under its most recent concept (Chatzimanolis *et al.* 2010; Brunke *et al.* 2015) comprises a diverse and species-rich monophylum forming a predominant type of rove beetles in the mesophilic habitats of the highly disjunct south temperate areas of the globe. Based on a rather basal position of the Amblyopinina in the phylogenetic tree of Staphylinini, fossil-inferred age of this tribe, and the distribution pattern of tentative amblyopinine monophyletic lineages, early diversification of this group is associated with the Gondwana-derived South America-Antarctica-Australia-New Zealand landmass before its fragmentation. Mammal-associated, morphologically highly derived species constitute a minority within Amblyopinina and they are mainly confined to South and Central America. Existing evidence suggests that American mammal-associated amblyopinines form a fine tuned mutualistic relationship with the mammal hosts by feeding on their ectoparasites.

Myotyphlus, endemic to Australia, is the only mammal-associated amblyopinine outside America. The genus comprises at least three species diagnosable by the shape of the aedeagus two of which, *M. newtoni* sp. nov. and *M. wurra* sp. nov., occur sympatrically in the south-western Australia, and one, *M. jansoni*, is confined to Tasmania. Most specimens of *Myotyphlus* were collected from the bodies of small mammals, rodents and one marsupial, while some – in bat guano in the caves. There seems to be no strict association with one particular mammal species in any of three *Myotyphlus* species. Larvae of *Myotyphlus* are unknown and it is unclear how long and when any of its species occur on mammal hosts during their life cycle.

Current state of knowledge suggests that mammal mutualistic *Myotyphlus* has an independent origin from the Neotropical mammal mutualists, and even within the latter different genera could have originated from independent free living lineages. Presumably *M. jansoni* has originated from a species of free living Australian Amblyopinina. Highly reduced eyes in *Myotyphlus* and South American *Edrabius*, a feature contributing to their similarity and causing earlier views about phylogenetic affinity of both genera, seems as a convergent adaptation to caves in the case of *Myotyphlus* and nocturnal, mammal and/or mammal-burrow associated behavior in the case of *Edrabius*.

Although sister group relationship of *Myotyphlus* remain to be rigorously explored, it is logical to assume that its association with mammals in Australia evolved a relatively short time ago, after the colonization of the Australian continent by rodents and dasyurine carnivorous marsupials. The distinctly less specialized morphology of *Myotyphlus* compared to the mammal-associated species from the Neotropical region, is consistent with relatively shorter time of existence there of its mammal hosts providing therefore shorter evolutionary time for *Myotyphlus* to develop its co-adaptations with mammals. It is not clear if the rodent-associated lifestyle was primary with subsequent shifts to guano dwelling in caves via their rodent hosts visiting caves. Or the adaptation to guano-associated biology in caves was the original state for *Myotyphlus*, serving as a precondition for the next evolutionary step towards an association with rats, frequently seeking shelter in caves and thus getting into proximity with guano-dwelling beetles there.

An ongoing generic revision of free-living Amblyopinina and a molecular phylogeny of the subtribe will hopefully provide a baseline to further investigate the sister-group relationships of *Myotyphlus*. In addition, phylogenetic reconstruction of the Neotropical mutualistic Amblyopinina and their hosts has the potential to reveal the level of congruence between both sides of a mutualistic relationship and provide an insight into the origin(s) of the unique relationship.

Insect-mammal cases of mutualism are very rare and, apart from Amblyopinina rove beetles, is known for *Cryptoses* moths and sloths in South America. Other staphylinoid beetle, Holarctic *Platypsyllus castoris* (Leiodidae), that is thought to be parasitic on beavers, may in fact be mutualistic similarly to Amblyopinina. The example of *Myotyphlus* has some similarity with a rare case of *Arixenia* earwig and *Cheiromeles* bat interaction that perhaps is also a case of mutualism.

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Figures

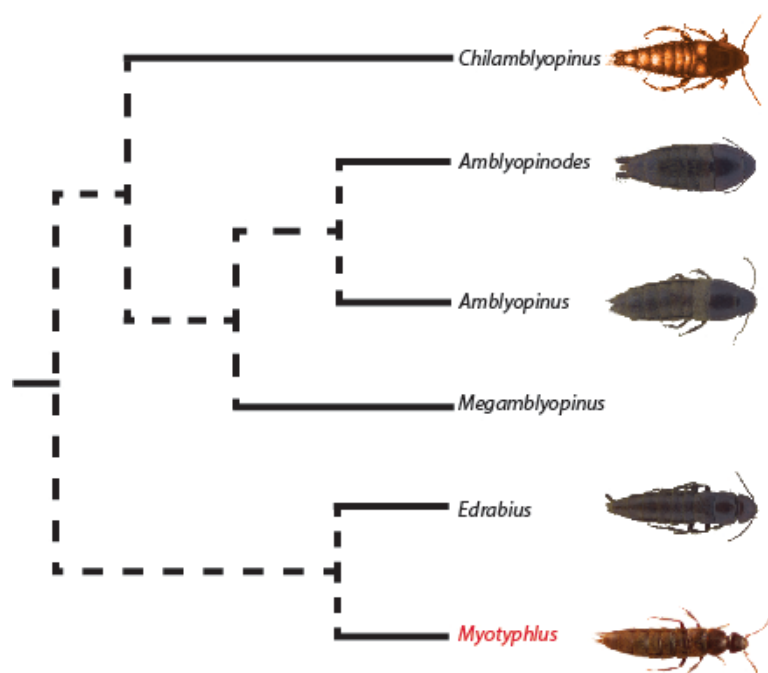


Fig. 1. Schematic phylogeny of the tribe Amblyopinini expressing the ideas of Ashe and Timm (1988). Illustrated are: *Chilamblyopinus piceus*, adapted from the illustration of Ashe and Timm (1988), *Amblyopinodes* sp. from Brazil, *Amblyopinus jelskii* Solsky, 1875, *Edrabius kuscheli* Scheerpeltz, 1957 from Chile and *Myotyphlus* sp. (female) from Australia.

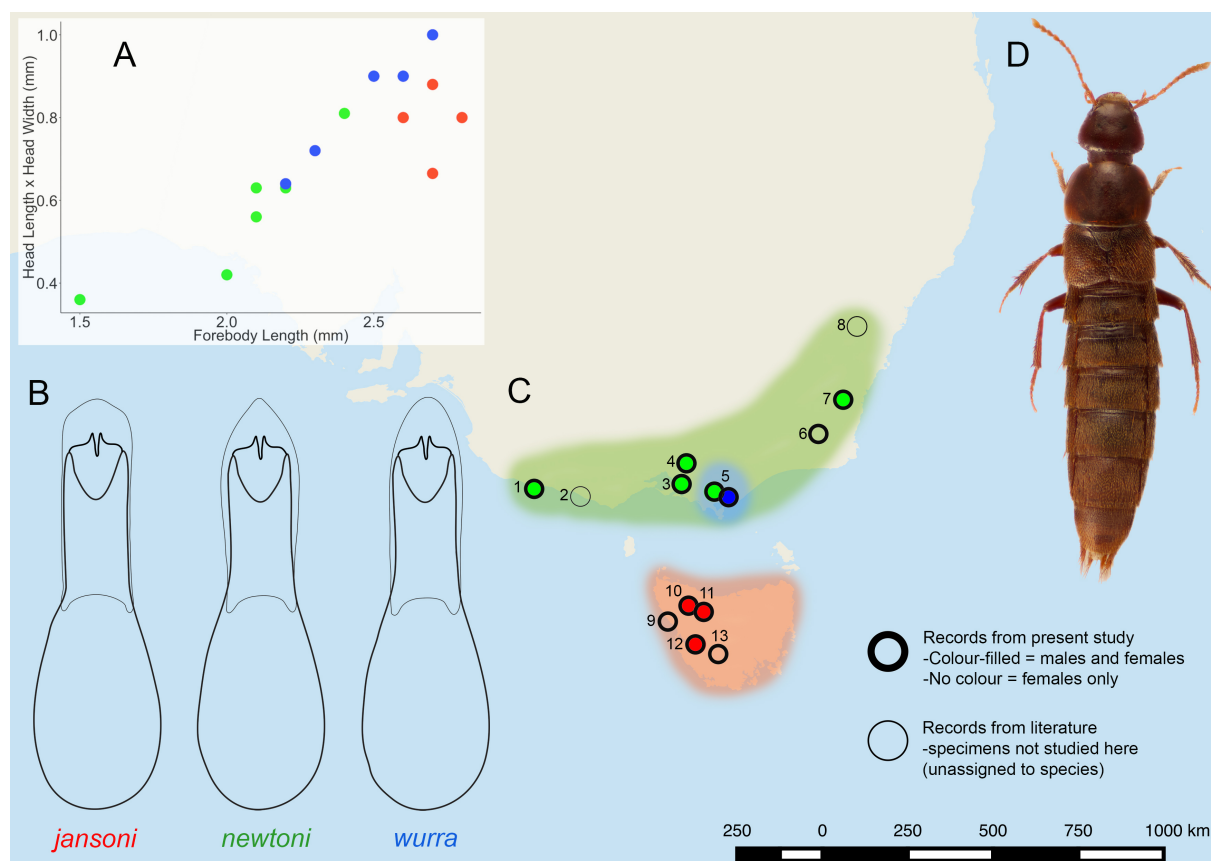


Fig. 2. A - The relationship between Forebody Length (mm) and Head Length x Head Width (mm) for three species of *Myotyphlus*: *M. jansoni* (red), *M. newtoni* **sp. nov.** (green) and *M. wurra* **sp. nov.** (blue). **B** – Aedeagi of *Myotyphlus jansoni*, *M. newtoni* and *M. wurra*. **C** – distribution of specimens and species studied in this paper (thick circles) and records from literature (thin circles). Colours in circles correspond to those used in 2A and B. Corresponding shaded areas indicate hypothesized distribution of respective species based on locality data so far available. **D** – habitus of female *Myotyphlus* sp. from Olson's Bridge, Victoria.

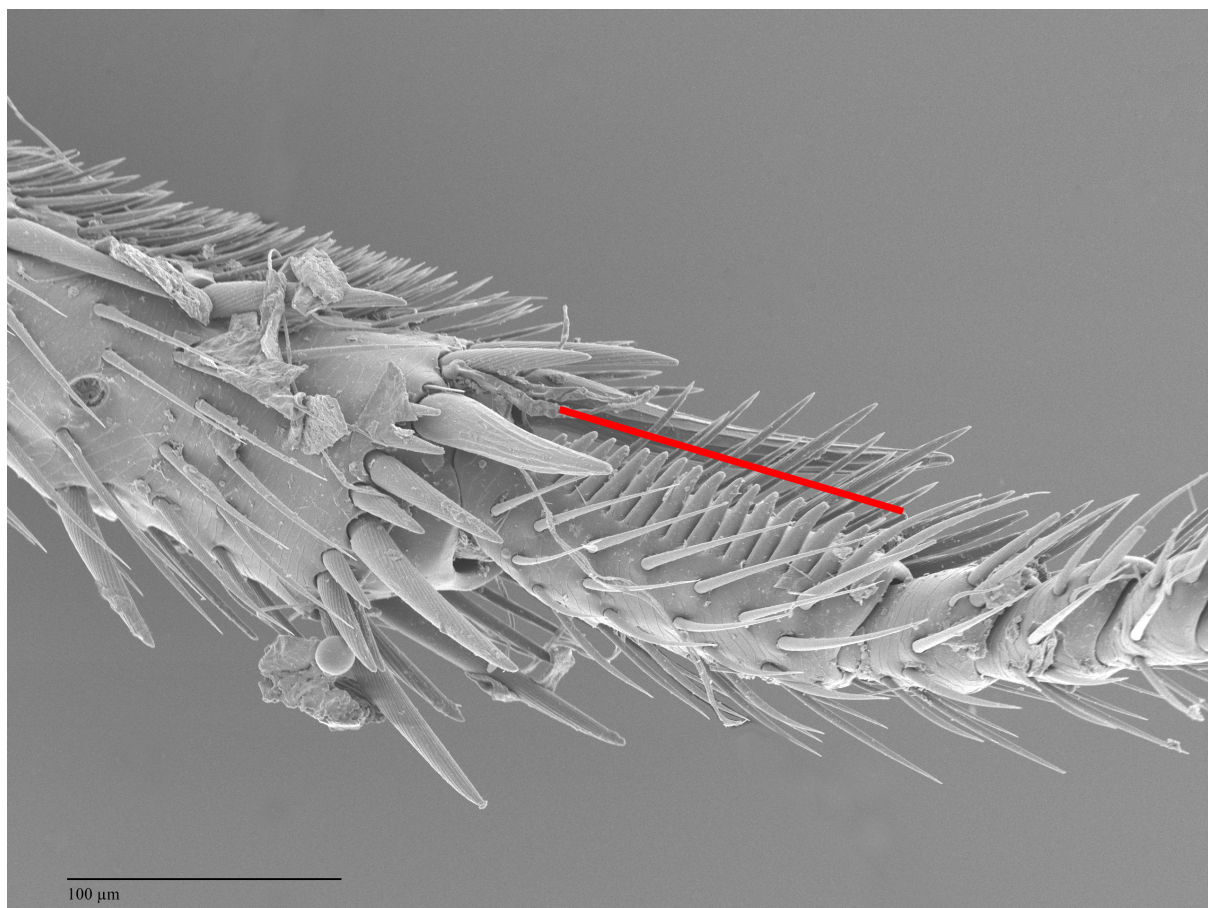


Fig. 3. Mesotarsus of *Myotyphlus jansoni* (female) from Tasmania showing the comb on the first tarsomere (red line). Scale bar = 100 micro metres (μm).

798 **Table. 1.** Synthesis of *Myotyphlus* species and associated data used in this study. ^a= records
 799 from Hamilton-Smith and Adams (1966) and personal communication therein. Locality, Date,
 800 Host and Collector data are repeated verbatim from data labels beneath specimens or from
 801 literature.

Species	Locality	State	Date	Male s	Putative Female s	Host	Collector	Locality (number on map)
<i>M. jansoni</i>	Cradle Mt	Tasmania	6.xiii.1964	1	1	<i>Pseudomys higginsii</i>	R.H. Green	10
<i>M. jansoni</i>	Franklin River, below Gordons Peak	Tasmania	15 Jan. 1983	2	-	-	E.B. Britton	12
<i>M. jansoni</i>	Mt Kate	Tasmania	16.x.1964	1	1	<i>Rattus lutreolus</i>	R.H. Green	11
<i>M. jansoni</i>	Florentine Valley	Tasmania	7.vii.1959	-	1	<i>Rattus lutreolus velutinus</i>	B.C. Mollison	13
<i>M. jansoni</i>	Corinna	Tasmania	8.ii.1965	-	1	<i>Antechinus swainsonii</i>	R.H. Green	9
<i>M. newtoni</i>	Olson's Bridge	Victoria	11-9-59 (Sept)	2	-	<i>Rattus assimilis</i>	R.M Warneke	5
<i>M. newtoni</i>	Loch Valley	Victoria	27.vii.63	1	-	In fur of <i>Rattus assimilis</i>	R.M Warneke	4
<i>M. newtoni</i>	Deua NP, Deua Cave	New South Wales	5 Apr. 1986	1	-	Bat guano	E. Holm	7
<i>M. newtoni</i>	French Island	Victoria	29.viii.1967	1	1	<i>Rattus fuscipes assimilis</i>	R.M Warneke	3
<i>M. newtoni</i>	Bat's Ridge	Victoria	20.i.1968	1	1	<i>Rattus assimilis grayii</i>	J.H. Seebeck	1

<i>M. wurra</i>	Olson's Bridge	Victoria	7.vii.1959	5	-	<i>Rattus assimilis</i>	R.M Warneke	5
<i>Myotyphlus sp.</i>	South Ramshead, 1850m, Kosciuskco Nat. Pk.	New South Wales	May 1981	-	1	-	Ken Green	6
<i>Myotyphlus sp.</i>	Olson's Bridge	Victoria	7.vii.1959	-	3	<i>Rattus assimilis</i>	R.M. Warneke	5
' <i>M. newtoni</i> ' ^a	Lake Gilleear Guano Cave near Warrnambool	Victoria	May 13, 1962 May 19, 1973 Jan 12, 1964	-	-	Bat guano of <i>Miniopterus schreibersi</i> (Kuhl)	-	2
' <i>M. newtoni</i> ' ^a	Southern Limestone (cave), Jenolan	New South Wales	July 25 1964	-	-	Bat guano of <i>Miniopterus schreibersi</i> (Kuhl)	B. Dew	8